

TRISTICHOGRAPTUS, A TRISERIAL GRAPTOLITE FROM THE LOWER ORDOVICIAN OF SPITSBERGEN

by R. A. FORTEY

ABSTRACT. The structure and development of *Tristichograptus* [formerly *Trigonograptus*] *ensiformis* (J. Hall) is described, from relief material, from the Lower Ordovician Valhallfonna Formation, Spitsbergen. It is the only known triserial graptolite, but appears 'biserial' when flattened. The relation of *Tristichograptus* to *Phyllograptus*, *Tetragraptus*, and biserial graptolites is discussed.

FOR many years the genus *Tristichograptus* Jackson and Bulman has been known under the name of *Trigonograptus*, principally from the species *T. ensiformis* Hall, of wide distribution in the Lower Ordovician. It has recently become apparent that the type specimen of the type species of *Trigonograptus*, *T. lanceolatus*, comprises two stipes of a *Didymograptus* lying side by side (Jackson and Bulman 1970). The distinctive *T. ensiformis* obviously merits generic recognition and the new name *Tristichograptus* was proposed by Jackson and Bulman with *T. ensiformis* as the type species.

Although widely known from flattened specimens, the structure of this form has hitherto remained obscure. Recently collected material from the Valhallfonna Formation, Northern Ny Friesland, Spitsbergen (Vallance and Fortey 1968) contains specimens preserved in full relief, which have enabled the structure of *T. ensiformis* to be elucidated. The graptolite occurs between 147 m and 157 m above the base of the formation in a dark, impure limestone; it is only abundant in one thin limestone bed at 147 m and the specimens figured in this paper all come from this horizon. *T. ensiformis* is associated with numerous trilobites of the families Olenidae (*Triarthrus*, *Hypermecaspis*, and cf. *Parabolinella*), Endymioniidae (*Endymionia*), and Komaspidae (*Carolinites*); conodonts, chitinozoa, scolecodonts, and rare inarticulate brachiopods were also obtained on dissolving the rock. Most of the graptolite material is heavily carbonized and disintegrates when the matrix is dissolved. Certain irregular patches of the rock are silicified and this seems to have protected the graptolite periderm from further diagenetic changes. When this siliceous rock is dissolved in hydrofluoric acid, all traces of carbonate having been removed in dilute acetic acid, large pieces of the rhabdosome could be obtained, sometimes quite clear, or easily cleared.

SYSTEMATIC DESCRIPTION

Family DICHOGRAPTIDAE Lapworth 1873

Genus TRISTICHOGRAPTUS Jackson and Bulman 1970

Tristichograptus ensiformis (J. Hall)

Plates 26-29

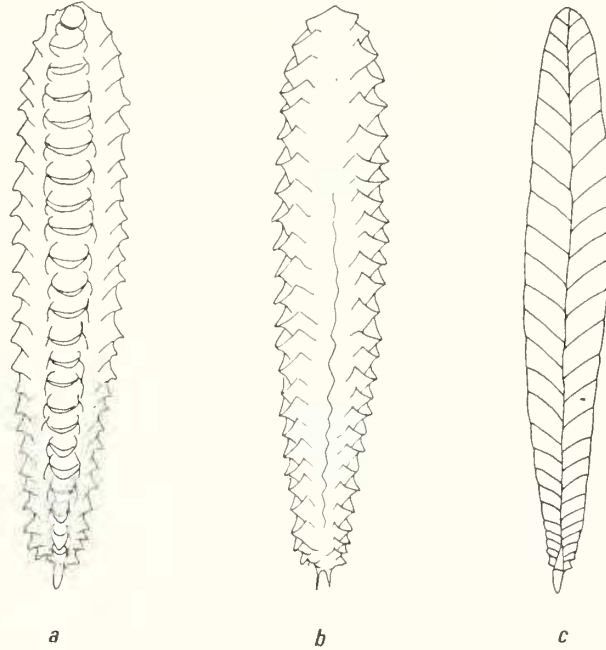
1858 *Graptolithus ensiformis* Hall, p. 133.

[Palaeontology, Vol. 14, Part 1, 1971, pp. 188-199, pls. 26-29.]

Material (numbers refer to the Sedgwick Museum, Cambridge catalogue). Complete growth series: SM A70588-94, 70598; isolated distal fragments: SM A70595, 70586-7; specimens in relief on the rock: SM A70582-5; other material: more than 100 isolated proximal and distal fragments.

Horizon and locality. Lower Ordovician, Valhallfonna Formation, Lower limestone division, 147 m above base, N. Ny Friesland, Vestspitsbergen.

Description. The rhabdosome is triserial, scandent, lanceolate, tapering gently proximally, more rapidly distally (text-figs. 1-3). There is no nema after the first four or five thecae of each series have been developed. The three series of thecae are set at 120°

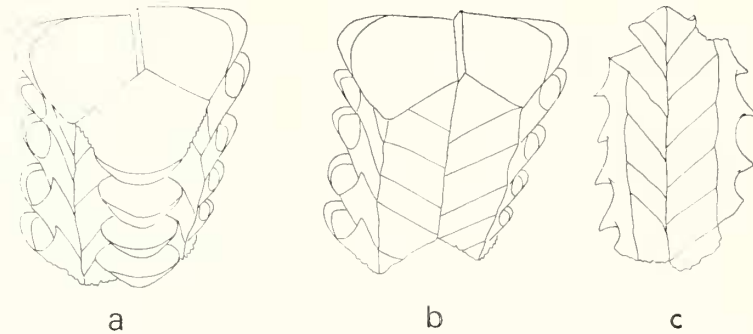


TEXT-FIG. 1. Reconstruction of complete rhabdosome. $\times 4$. *a.* Apertural view. *b.* Lateral view. *c.* With one series removed to show typical appearance of flattened material. Compare Pl. 29, fig. 3*a.*

to one another, and the cross-section of the stipe is a rounded triangle (text-fig. 2*a*) the apices of the triangle being formed by the apertural lips of the thecae. The width of the stipe (that is, the side of the cross-sectional triangle) gradually increases up to about 3-4 mm at th. 11, though the mature width is somewhat variable. The length of the rhabdosome rarely exceeds 20 mm. In the mature parts of the stipe the thecae are spaced 10-12 in 10 mm, 11 being usual, but are more closely spaced proximally, the first 3 mm of each series enclosing 5 thecae.

The thecae are inclined at 40-50°, slightly less proximally. They are short and broad with a maximum transverse width of 1.25 mm and have downwardly deflected lips 0.5 mm in length. Thecal overlap is 0.5-0.6. In profile the apertural margin is gently undulate. The thecae in the mature stipe are connected with succeeding thecae in the

same series by transversely elliptical foramina with thickened margins, 0.6 mm long diameter and 0.2 mm wide. The growing end of the mature rhabdosome is arranged in a clockwise spiral of thecae, that is, each thecae to the left is displaced upwards one third of the interthecal spacing. The contact of one series of thecae with the others is along an apparent median septum, which forms the perpendicular bisectrix of the cross sectional triangle (text-fig. 2*a*): it is thus triradiate with the three walls set at 120° to one another. Each series retains a complete, dorsal peridermal wall, so that the septum is composed of a double layer of periderm. Because of this any one series of thecae may easily be detached from the other two.

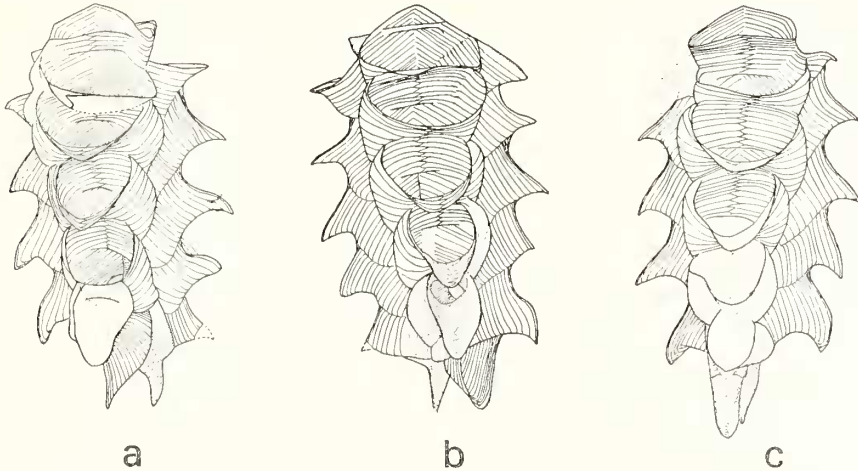


TEXT-FIG. 2. Derivation of an apparently biserial from the triserial rhabdosome, partly schematic. *a*. Part of mature rhabdosome. *b*. The same, with third series broken off along the median septum, to give an apparently biserial rhabdosome. Note alternating arrangement of the traces of the interthecal septa of the remaining two series. *c*. Dorsal view of specimen derived as *b*. $\times 12.5$. SM A70599.

When one series of thecae are separated along the 'median septum', which generally happens when rock containing relief material is broken, the resulting appearance of the rhabdosome is identical to that of previously published figures of *T. ensiformis* (see text-fig. 2*b*; Pl. 29, figs. 2, 3; text-fig. 1*c*). In this case only the two surfaces of the 'median septum' set at 120° can be seen with the traces of the interthecal septa of the two remaining series of the upper surface. The interthecal septa are alternate, displaced about one third the interthecal distance on either side of the 'axis', corresponding to the spiral order of the thecae of the rhabdosome. The apertures are not visible in this aspect, and so an apparently *biserial* graptolite is seen with a nearly straight sided margin.

All material of *T. ensiformis* known hitherto is flattened, and it is important to consider how flattening can reduce the three stiped graptolite to a 'biserial' appearance. The rhabdosome would usually come to rest on the sediment surface on one of its three sides. This results in the third thecal series pointing vertically (text-fig. 2*a*). The principal plane of weakness then lies along the plane of the 'median septum', the rhabdosome splitting along this nearly horizontal plane more easily than around the projecting thecae (text-fig. 2*b, c*; Pl. 29, fig. 3). Flattening opens out the median septum from 120° to 180°. The lower two series of thecal apertures are directed downwards and obscured by the 'median septum', and the third series also cannot be seen as it is pointing upwards into the rock containing the counterpart. The collapse of the thecal margins of the

bottom two series of thecae results in the almost straight sided 'edge' of the flattened *Tristichograptus*. Thus *Tristichograptus ensiformis* as seen when flattened is, in fact, merely part of the 'median septum', with the traces of the interthecal septa of the bottom two series only, forming the two series of the apparently biserial rhabdosome. This mode of preservation carries with it the implication that tristichograptids with different apertural characteristics could give similar compressions.



TEXT-FIG. 3. Three aspects of a small mature rhabdosome. $\times 25$. *a.* Series *a* apertural view. *b.* Series *b* apertural view. *c.* Series *c* apertural view. This specimen was broken on transference to glycerine. SMA70588 represents the similar stage of growth.

Elles and Wood (1908) seem to have come some way towards an understanding of the arrangement of the thecae when they commented that the 'two stipes' may have been arranged at right angles, 'rather like a *Phyllograptus* with only two of the stipes developed'. One of their figured specimens shows a prominent 'virgellar spine': this could be developed simply from the compression of that aspect in which the sicula, th. 1¹ and th. 1² lie in the same plane (text-fig. 3*c*).

Discussion. Published measurements of *Tristichograptus ensiformis* (Table 1) are in general agreement with those obtained from the Spitsbergen material (based on 30 specimens). Both 'width' and length are highly variable; those specimens with greater width are also much longer than the Spitsbergen material (e.g. Ruedemann 1947) and such differences merely seem to reflect continued growth rather than specific differences. The thecal spacing varies from 9 to 12 in 10 mm, the majority have a mature spacing of 11 in 10 mm; the Spitsbergen material agrees well. The inclination of the thecae to the 'axis' is also close to previously described examples. It seems reasonable to conclude that, in so far as the measurements made on flattened *Tristichograptus* reflect the characters of the whole rhabdosome, the described material does represent a single species.

There is little variation in the shape of the thecae of isolated material; some specimens have slightly narrower thecae proximally than others (text-fig. 5). One remarkable

pathological fragment (Pl. 28, fig. 2) has the thecae arranged in a T-shape, like three series of a *Phyllograptus*; distally it degenerates into an irregular cluster of 5 relatively small thecae. In spite of its bizarre appearance the shape of the thecae leave no doubt that this is an abnormal *Tristichograptus*.

TABLE 1

Author	Max. length (mm)	Max. 'width' (mm)	Proximal no. of thecae 10 mm	Distal no. of thecae 10 mm	Angle of inclination of thecae
Hall 1865	60	4		11	50
Hopkinson and Lapworth 1875	8	2		12	
Nicholson 1890	15	3			
Elles 1898	38	4.76	11	9-10	45
Elles and Wood 1908	50	5		9-11	50
Harris 1924		5		11	45
Ruedemann 1947	80	7		11	45
Mu and Lee 1958	35	4	12	10	30-50
" " " (var. minor)	16	2.4	14	9-10	
Berry 1960	50	3		9-11	45
Obut and Sobolevskaya 1964	18	4		10-11	50-55
Yao 1965	40	4		11	30-50
Fortey (this paper)	21	4	12-16	10-12	40-50

The genus *Pseudotrigonograptus* Mu and Lee (1958) compares closely with *Tristichograptus* in stipe width, thecal spacing and form of 'theca' (i.e. the median septum with the traces of interthecal septa). Mu and Lee believed that this form had four stipes like *Phyllograptus*, but with thecae in adjacent rows in contact along their length as in *Tristichograptus*. To judge from the illustrations of relief material of *Pseudotrigonograptus* (Mu and Lee 1958), and from the fact that *Trigonograptus ensiformis* is recorded from the same beds, there seems little reason to doubt that *Pseudotrigonograptus* is synonymous with *Tristichograptus*. Mu and Zhan (1966) reached the same conclusion, but believed *Trigonograptus* itself to be a quadriserial, *Phyllograptus*-like form.

Development (Pls. 26-28). A number of nearly clear growth stages were obtained from which the proximal and development could be deduced. The prosicula is 0.25-0.3 mm

EXPLANATION OF PLATE 26

Proximal end development of *Tristichograptus ensiformis*. $\times 50$.

Fig. 1. Prosicula and early metasicula. SM A70598.

Fig. 2. Sicula and initial bud, showing origin of th. 1¹ on prosicula. SM A70589.

Fig. 3a. Mature sicula and first theca showing origin of th. 1². SM A70590. 3b. Thecal diagram.

Fig. 4a. Growth stage showing origin of th. 2¹. SM A70591. 4b. Thecal diagram.

Fig. 5a. Growth stage showing origin of th. 2². SM A70592. 5b. Thecal diagram.

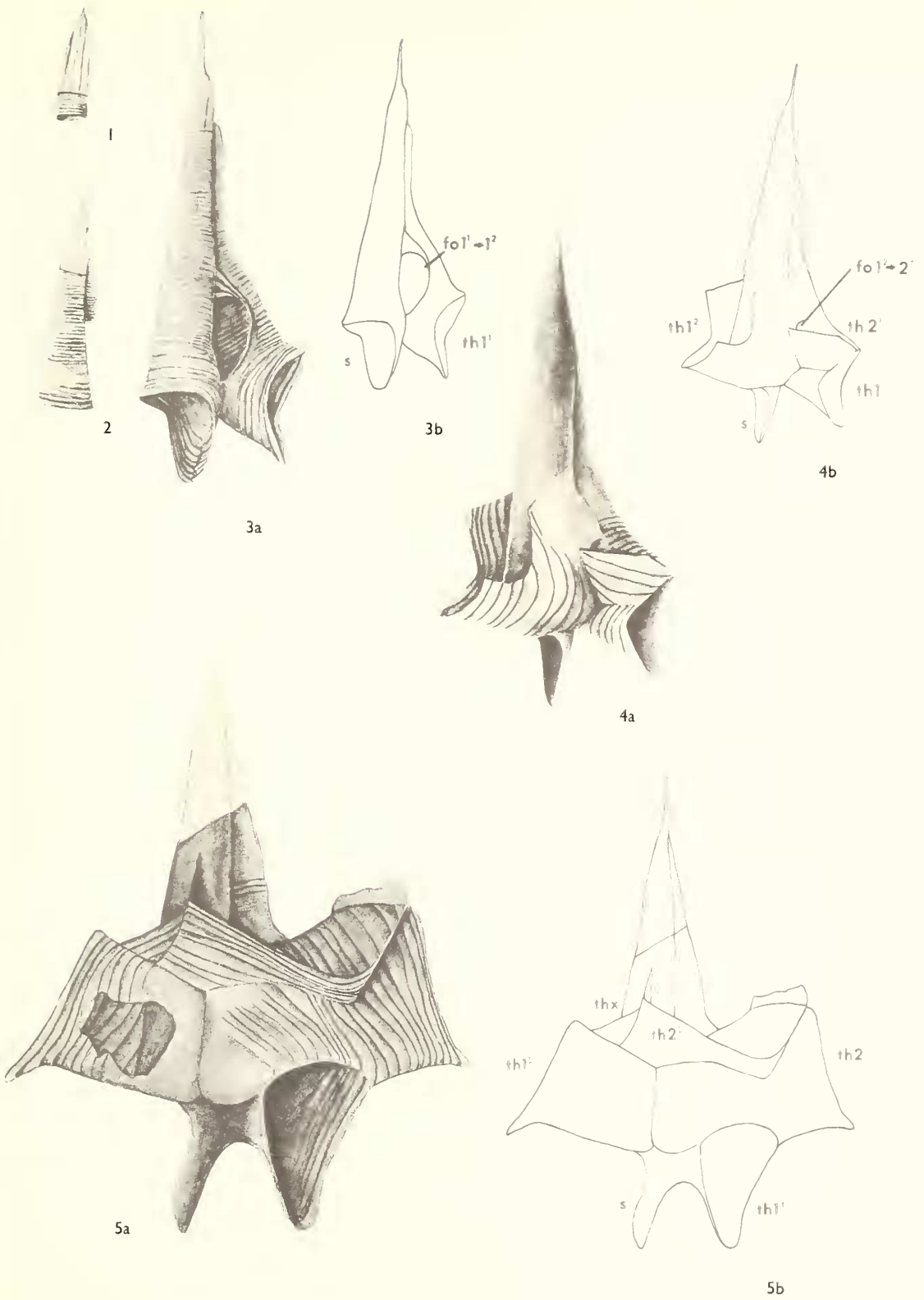
All figures in *b* apertural aspect. fo = foramen; s = sicula.

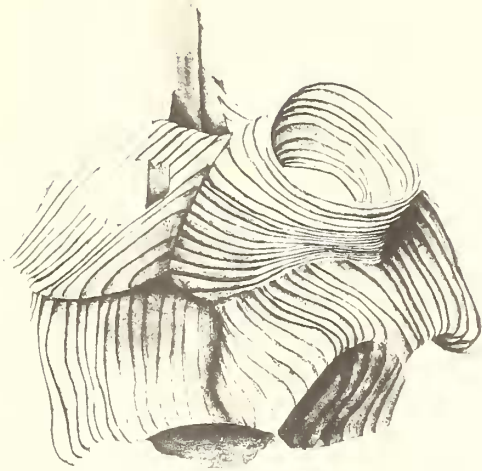
EXPLANATION OF PLATE 27

Proximal end development of *Tristichograptus ensiformis*, $\times 50$. SM A70593. Growth stage showing origin of th. 3^{1a} and th. 3^{1b}.

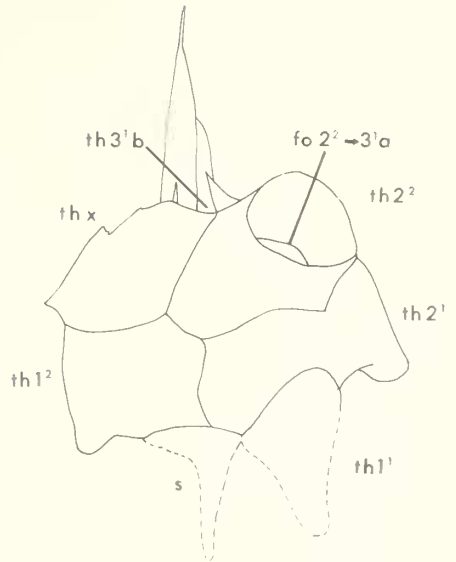
Fig. 1a. Series *b* apertural aspect. 1b. Thecal diagram.

Fig. 2a. Series *a* apertural aspect. 2b. Thecal diagram. fo = foramen; s = sicula.

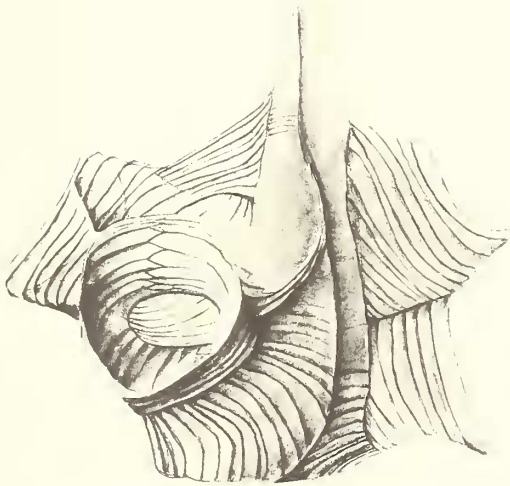




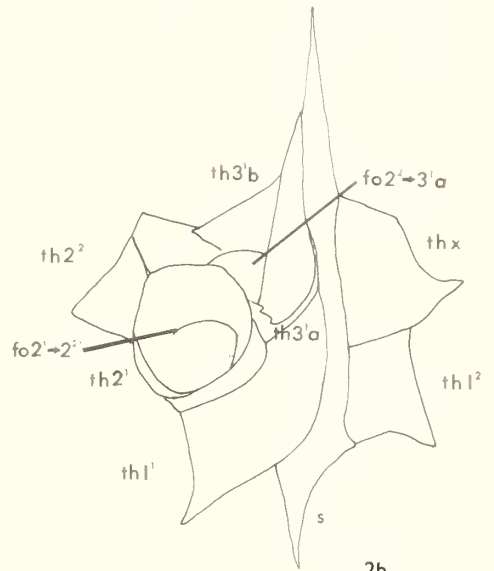
1a



1b



2a



2b

long with a hollow nema 0.05–0.1 mm long; there are 7 or 8 longitudinal lines (Pl. 26, figs. 1, 2). The distal margin of the prosicula seems to have a slightly thickened rim. The mature sicula attains a length of 1.6–1.9 mm; it curves slightly distally and is produced ventrally into a long, narrow spatulate lip up to 0.5 mm long (Pl. 26, fig. 3). The aperture is circular, 0.30 mm in diameter. The initial bud (Pl. 26, fig. 2) appears about two thirds of the way down the prosicula from a ventral, circular, resorption foramen. It is developed when the metasicula is only 0.15 mm long; thereafter the first theca grows down the ventral side of the sicula until almost on a level with the sicular aperture, when it is flexed sharply away from the sicula lip to form an angle of 45–60° with the ventral side of the sicula. The lip of th. 1¹ is not usually so pronounced as that of the sicula, 0.3 mm long. It is noteworthy that the growth-lines on the sicula and first theca are relatively densely spaced compared with those of the thecae that follow; moreover the sicula and th. 1¹ become secondarily thickened at a very early stage so that the growth-lines soon become difficult to discern. The second thecae, th. 1², originates from a foramen 0.35 mm high, half-way down th. 1¹, grows ventrodorsally across the sicula to point in the opposite direction to th. 1¹ (Pl. 26, figs. 3, 4). The circular aperture with a prominent lip is similar to that of th. 1¹. The sicula, th. 1¹ and th. 1² and their apertural lips lie in the same plane, and the lips project below the rest of the stipe: there is as yet no tendency for the thecae to become scandent.

The development becomes complex subsequently, and it is difficult to refer the succeeding thecae to the conventional scheme of thecal nomenclature. The three series have been named *a*, *b*, and *c*, and these are recognized as follows: series *c* is that series which is most closely aligned with th. 1²; series *b* is that series which is most closely aligned with th. 1¹; series *a* is that series which is not aligned either with th. 1¹ or th. 1². When the rhabdosome comes to rest on one of its three sides one of these three series points upwards. The three aspects of a small mature stipe are shown in text-fig. 3.

A foramen is produced very near to the base of th. 1², to give rise to th. 2¹ (Pl. 26, fig. 4). This theca develops into the first evidence of the triserial arrangement, growing across the dorsal side of th. 1¹ (Pl. 26, fig. 5) to form the basal theca of series *a*. A second foramen in th. 1² gives rise to th. *x* (series *c*) shortly afterwards; this theca continues to grow almost in line with th. 1² for some time. Thus th. 1² is dicalycal, and establishes the first thecae in series *c* and *a*. Th. *x* is remarkable in that it does not give rise to any of the succeeding thecae. The first theca of series *b*, th. 2², originates near the proximal end of th. 2¹ (Pl. 26, fig. 5). The basic triserial pattern of the rhabdosome has now been established, but a peculiar feature of the subsequent development is that the second thecae of series *a* and *c* are not derived directly from the preceding thecae in the same series. Th. 2² thus forms the base from which the rest of the rhabdosome develops. The following three thecae originate in quick succession as follows; in *b* apertural aspect (Pl. 27, fig. 1) a right lateral foramen in th. 2² gives rise to th. 3^{1a} (Pl. 27, fig. 2); th. 3^{1b} originates via a dorsal foramen also in th. 2² (Pl. 27, fig. 1); shortly afterwards th. 4^{1c} is derived from th. 3^{1b} (the foramen showing this is illustrated in *c* apertural aspect in Pl. 28, fig. 1). Th. 3^{1b} also gives rise to the succeeding theca in the same series, th. 4^{1b}. Th. 2² and th. 3^{1b} are thus both dicalycal. The sicula is not centrally placed throughout this development, but is closer to series *c* than to series *a* or *b*, that is away from the side in which the branching is taking place (Pl. 27, figs. 1, 2).

The triserial arrangement that characterizes the mature stipe has now been established,

and series *a*, *b*, and *c* remain separate; th. 4^{1c} gives rise to th. 5^{1c}, etc., th. 3^{1b} to th. 4^{1b}, 5^{1b}, etc., th. 3^{1a} to th. 4^{1a}, 5^{1a}, etc. No evidence of a nema has been seen above the level of about th. 5.

The interthecal septum where it has been observed is a single unit formed by the dorsal wall of the lower of two thecae in contact (for example, that between th. *x* and th. 4^{1c}, Pl. 28, fig. 1). The thecae change in form gradually over the proximal part of the stipe, having progressively less circular, more transversely elliptical apertures (text-fig. 3, Pl. 29, fig. 4) of increasing diameters, and the thecal lips becoming proportionately shorter. The first four thecae are not precisely aligned with those in the distal part of the rhabdosome (Pl. 29, fig. 5). The rhabdosome becomes thickened with cortical tissue progressively upwards from th. 1². The development is shown diagrammatically in text-fig. 6.

Accessory foramina. When the rhabdosome is dissected or fortuitously broken, additional foramina have been observed in apparently constant positions. They are smaller than the normal foramina, sub-circular, with a slightly thickened rim. One dissected specimen is shown in text-fig. 4, from which parts of the external walls were removed using fine forceps to reveal the internal structure. The accessory foramen between th. *x* and th. 4^{1c} is formed in the dorsal wall of th. *x* in such a position that it could not have given rise to th. 4^{1c}. Growth-lines on th. *x* are truncated by the foramen, and it must, therefore, have been formed by resorption, in a manner analogous to the primary resorption foramen, but unlike the foramina involved in the development described previously. Similar foramina are developed between th. 2² and th. *x*, and between th. 3^{1b} and th. 4^{1a}. Their development is apparently constant and in the same positions; we have seen three examples of that between th. 2² and th. *x*, two of that between th. *x* and th. 4^{1c}, but only one of that between th. 3^{1b} and th. 4^{1a}. It remains a possibility that they may be found in other positions.

Probably the only comparable structure known is the foramen produced between

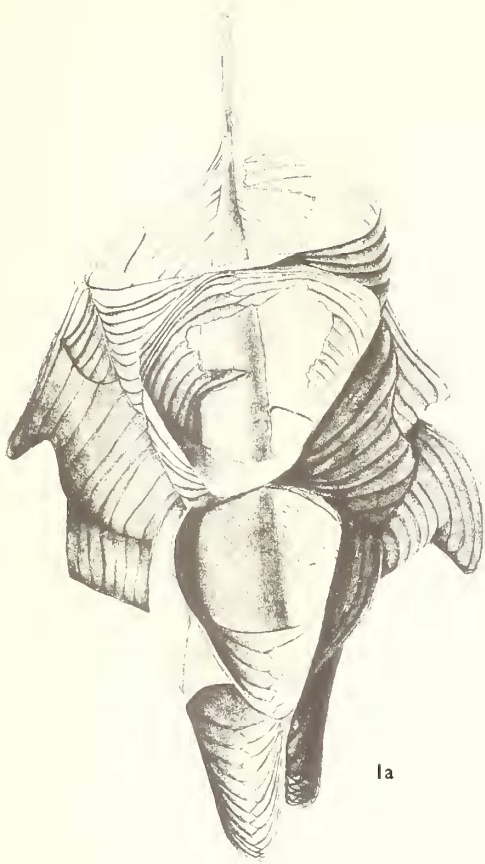
EXPLANATION OF PLATE 28

- Fig. 1a. Growth stage of *Tristichograptus ensiformis*, ×50. SM A70594. Series *c* apertural aspect, showing origin of th. 4^{1c}. 1b. Thecal diagram. fo = foramen; s = sicula.
 Fig. 2. Pathological specimen, ×25. SM A70595.

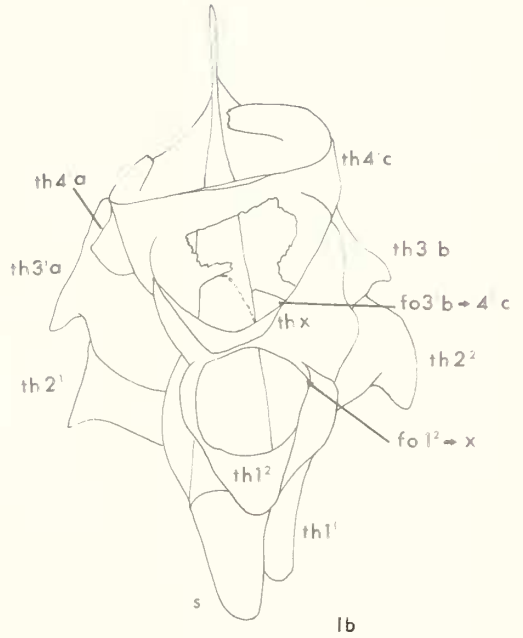
EXPLANATION OF PLATE 29

Tristichograptus ensiformis.

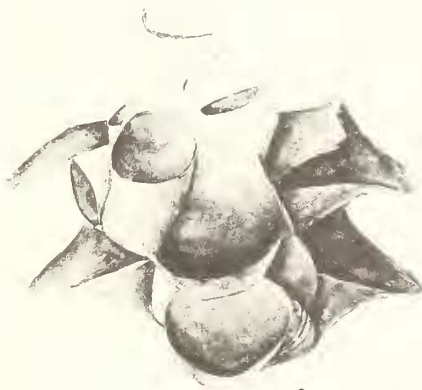
- Fig. 1. Isolated distal fragment, ×6. SM A70587.
 Fig. 2. Specimen with third series partly broken out, but visible in the proximal part of the rhabdosome. ×6. SM A70585.
 Fig. 3a. Nearly complete rhabdosome with third series broken out to show the typical appearance of *Tristichograptus* as known from flattened material. ×6. SM A70583.
 Fig. 3b. Distal fragment, third series only, the other two series having broken out along median septum. ×6. SMA 70584.
 Fig. 4. Isolated small, complete rhabdosome. Series *a* apertural aspect, ×15. SM A70588.
 Fig. 5. Isolated near-proximal fragment, ×10. SM A70586.
 Fig. 6. Distal fragment, lateral view, ×6. SM A70582.
 Figs. 1, 4, 5, photographed beneath glycerine; in Figs. 2, 3, 6, the specimen was whitened with ammonium chloride.



1a



1b



2